Marten Habitat Selection in a Clearcut Boreal Landscape

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Abstract: *To describe the forest mosaic suitable for marten (*Martes americana*) in a clearcut boreal landscape, we studied habitat selection in an area (123 km^2) located in western Québec, in which black spruce (*Picea mariana*) was the predominant forest type. This block had been recently clearcut with the protection of regeneration cutting technique, a logging method that employs equally spaced harvesting trails. The resulting landscape had a center dominated by a cutover matrix (60% of the block) and surrounded by contiguous uncut forest. Over 2 years, 20 marten equipped with radio collars provided enough locations to delineate their winter home range. Habitat composition and spatial configuration were measured at both stand and landscape scales by means of a geographic information system database that included telemetry locations and home ranges, forest maps, and limits of clearcut areas. Inside their winter home ranges, animals avoided open regenerating stands composed mostly of recent clearcuts with sparse regeneration. They did not select coniferous stands, even those that were mature or overmature, but preferred deciduous and mixed stands, a large proportion of which had a dense coniferous shrub layer as a result of a spruce budworm (*Choristoneura fumiferana*) epidemic 15–20 years ago. At the landscape scale, winter home ranges differed from random mosaics because they had a larger proportion of uncut forest (>30 years), a smaller proportion of open regenerating stands, larger core area in forest habitat, and less edge between open regenerating stands and forest. Winter home ranges usually contained <30–35% open or closed regenerating stands and >40–50% uncut forest. We conclude that marten and clearcutting may be compatible, provided that forest logging is adapted to that species at the landscape level. Where the objective is to maintain marten at a local scale in black spruce forest, we suggest that ≥50% uncut forest be preserved inside 10-km^2 units and that <30% of the area be clearcut over a 30-year period.*

Selección de Hábitat por la Marta en un Paisaje Boreal Talado

Resumen: *Para describir un mosaico forestal viable para la marta (*Martes americana*) en un paisaje boreal con tala total estudiamos la selección del hábitat en un bloque de paisaje (123 km^2) localizado al oeste de Quebec, en el cual el abeto negro (*Picea mariana*) fue el tipo de hábitat predominante. Este bloque ha sido recientemente talado en su totalidad con la técnica de corte de protección de la regeneración, un método que emplea caminos de cosecha separados equidistantemente. El paisaje resultante tiene un centro dominado por una matriz de corte (60% del bloque) y está rodeado por un bosque contiguo sin cortar. Equipamos 20 martas con radiocollares por dos años, proporcionando suficientes localidades para delinear su rango de hogar para el invierno. La composición del hábitat y la configuración espacial fueron medidas a dos escalas (sitio y paisaje) utilizando una base de datos de GIS que incluyó ubicaciones por telemetría y rangos de hogar, mapas del bosque y límites de áreas de tala. Dentro de sus rangos de hogar del invierno, los animales evitaron los sitios abiertos en regeneración compuestos mayormente por talas recientes con regeneración dispersa. Las martas no seleccionaron los parches con coníferas, aún siendo maduros o viejos, pero prefirieron los sitios decíduos y mezclados, una larga proporción de los cuales tuvo una capa arbustiva densa de coníferas como resultado de una epidemia de hace 15 años del gusano del retoño del abeto (*Choristoneura

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fumiferana*). A escala de paisaje, los rangos de hogar difirieron de los mosaicos al azar debido a que existía una proporción de bosque sin cortar más grande (>30 años), una proporción más pequeña de sitios abiertos en regeneración, un área más grande de hábitat forestal y una menor cantidad de borde entre los sitios abiertos en regeneración y el bosque. Los rangos de hogar del invierno generalmente contenían <30–35% de sitios abiertos o cerrados en regeneración y más de 40–50% de bosque sin cortar. Concluimos que la marta y los clareos totales pueden ser compatibles, a condición de que la tala del bosque esté adaptada a esta especie a nivel de paisaje. Donde el objetivo es mantener las martas a una escala local en bosques de abeto negro, sugerimos que sea preservado ≥50% del bosque sin cortar dentro de unidades de 10 km^2 y que <30% del área sea talada a lo largo de un período de 30 años.*

Introduction

Ecosystem management has been proposed as a way to perpetuate the long-term integrity of original forest ecosystems by using scientific knowledge while accounting for socioeconomic needs (Grumbine 1994; Thomas & Huke 1996; Zeide 1998). Landscape-level management, which involves maintaining an appropriate mosaic of forest-stand age structures and spatial distribution (Oliver 1992), is needed to put that concept into practice. To implement landscape-level management, a "template" mosaic or model is needed that is based on the primitive forest and the historical range of natural variation (Rowe 1992; Booth et al. 1993; Franklin 1993). Defining this mosaic is difficult because the data are limited and the techniques tedious to apply on a landscape scale. Furthermore, our time reference period is short and the target mosaic is a moving one if we take into account anticipated climate changes (Hunter 1996).

Wildlife-habitat relationships also can be used to define model forest mosaics. Large predators such as the grizzly bear (*Ursus horribilis*), wolf (*Canis lupus*), or cougar (*Puma concolor*) might be an interesting group because they occupy vast areas (Beier 1993; Fritts & Carbyn 1995; Estes 1996). They are not very habitat-specific, however, and tend to be limited more by anthropic mortality (particularly wolves; Mladenoff et al. 1995), to be present at low density, and to be highly mobile, making their study difficult. The ideal candidate for an indicator species to define model forest mosaics should have large spatial requirements and use specific habitats. Recently, research on small forest carnivores has increased markedly (Buskirk et al. 1994), enhancing this group's suitability for the task. The American marten (*Martes americana*) has been described as a forest specialist in North America (Buskirk & Powell 1994) and has been viewed as a possible future emblem for old-growth boreal forests (Thompson 1991).

The marten is considered a species indicative of the "good health" of boreal forest in many jurisdictions (Bull et al. 1992; Buskirk 1992; Watt et al. 1996). This nonhibernating mammal is the only furbearing animal found in large numbers in mature forest (Thompson 1988). It preys mostly on small mammals and snowshoe hares (*Lepus americanus*) (Strickland & Douglas 1987). The marten has limited fat reserves (Buskirk & Harlow 1989), a long and thin body highly susceptible to heat loss that is nonetheless effective for sub-nivean and underground activities (Buskirk et al. 1988), and may be preyed upon by terrestrial mammals and larger birds of prey (Strickland & Douglas 1987; Hodgman et al. 1997). It has very large spatial requirements, with a home range proportionately three times larger than other terrestrial carnivores based on the mass-home range relationship (Buskirk & McDonald 1989; Lindstedt et al. 1986). To survive, martens must be selective in their choice of habitats.

The marten generally is associated with coniferous forest with a complex structure, mostly old, uneven-aged stands (Buskirk 1992; Buskirk & Ruggiero 1994). Results of studies in eastern North America support similar associations (Thompson 1988; Bissonette et al. 1989; Thompson & Harestad 1994; Sturtevant et al. 1996; but for a different viewpoint see Chapin et al. 1997). The marten has long been considered a species that is highly and negatively affected by forest logging (Marshall 1951). Thompson (1988) and Thompson and Harestad (1994) reviewed studies that document much lower population densities up to 40 years after logging. Recent research conducted in Maine, using geographic information system (GIS) analysis in a mixed forest landscape that was largely clearcut, concluded that martens need large patches of uncut forest and tolerate a small proportion of clearcuts in their home ranges (Chapin et al. 1998).

Clearcutting is the prevalent harvesting technique in the boreal forest. About 90% of the logging in Canada is done by clearcutting, amounting to an area of 10,000 km^2 per year (Gingras 1993). Management prescriptions proposed for the marten usually involve maintaining large tracts of mature forest (Bissonette et al. 1989; Lofroth & Steventon 1990; Thompson & Harestad 1994; Watt et al. 1996). These prescriptions are based on limited knowledge at the landscape scale and have not been tested in practice. Given the size of marten home ranges, there is a need to study and manage their habitat at the landscape level, the scale at which forest planning takes place (Bissonette et al. 1989; Buskirk 1992; Ruggiero et al. 1994*a*, 1994*b*). Some recent studies have used GIS to describe marten habitat at the landscape level (Katnik 1992; Lofroth 1993; McCallum 1993; Hargis 1996; Hargis & Bissonette 1997; Chapin et al. 1997, 1998). Except for Hargis (1996) and Chapin et al. (1998), however, only habitat composition—the proportion of each habitat type in the landscape—was evaluated in these studies. A true understanding of marten habitat requirements must also include spatial configuration attributes of the forest mosaic, such as patch size and shape, isolation, connectivity, and edge (Hunter 1990; Turner & Gardner 1991; Dunning et al. 1992; McGarigal & Marks 1995).

We report the results of a 2-year study conducted in a large boreal forest block where clearcuts were prevalent in the center of the landscape. We used radiotelemetry and GIS analysis to describe marten habitat selection. Our objective was to describe the forest mosaic suitable for the marten in that type of landscape. In contrast with Chapin et al. (1998), who conducted similar research in Maine mostly during the leaf-on season, our study focused on winter habitat and took place in an area more typical of the northern boreal forest. At the stand level, we hypothesized that in their winter home range martens would (1) avoid clearcut areas and (2) prefer mature or overmature coniferous stands. At the landscape level, we hypothesized that martens would select mosaics with (1) <20–30% area in clearcuts (based on the model of Thompson & Harestad 1994), (2) larger amounts of coniferous stands than that provided by a random selection in the overall study area, and (3) lower fragmentation than random mosaics, as indicated by landscape metrics related to patch shape, density, isolation, and edge. Movements and survival rates of martens in that block and in two controls are reported by Potvin and Breton (1997).

Methods

Study Area

Our study took place in a 123-km^2 block located in western Québec (lat 48°00′N, long 78°50′W). Black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*) are the dominant tree species. This area belongs to the balsam fir–white birch–white spruce (*Picea glauca*) ecological domain (Thibault 1985). Although black spruce is the prevalent forest cover type in our study area, the black spruce domain begins some 100 km to the north. Forest fires and spruce budworm (*Choristoneura fumiferana*) outbreaks are the major natural disturbances in this landscape (Bergeron 1991; Morin et al. 1993). The budworm primarily kills balsam fir trees but does not affect deciduous species. Forest logging in the area began at the turn of the century. At the end of our study, 29% of the land base was in coniferous stands, 11% in mixed stands, 7% in deciduous stands, 44% in regenerating stands (<20 years), and 10% in nonproductive areas (bogs, alder [*Alnus rugosa*] shrub stands). About one-third of the coniferous, mixed, and deciduous stands belonged to mature or overmature age classes (>80 years). The only regenerating stands of natural origin (6%) were openings created by the spruce budworm epidemic of 1974 to 1976 (Morin et al. 1993). Partial mortality by the budworm also converted mixed stands into deciduous or mixed deciduous stands. Most regenerating stands dated from 1992 to 1994, when 28% of the block was clearcut with the protection-of-regeneration cutting technique, a logging method that employs equally spaced harvesting trails to protect advanced regeneration (Fig. 1). The resulting landscape had a center dominated by a cutover matrix and surrounded by contiguous uncut forest (Fig. 2). In this matrix, the residual forest was fragmented and composed of narrow corridors 40–100 m wide along streams and permanent brooks or between individual clearcuts, and of small patches of uncut forest reserves, noncommercial young stands, and nonproductive areas. The total area where recent logging took place, including all clearcuts and the residual forest within or between clearcuts, amounts to 74 km^2, or 60% of the block. Martens were not trapped during our study. Based on trapping data (harvest/100 km^2), the marten population was stable in that region from 1989 to 1994 (Potvin 1998).

Habitat Selection Analysis

We used winter home ranges reported by Potvin and Breton (1997) to measure marten habitat selection. From August 1992 to December 1993, 33 animals (18 males, 15 females) were trapped and radiocollared. We located radiocollared animals from a Bell 206B helicopter. Locations were plotted on 1:20,000 topographic maps, and UTM coordinates were determined to ±20 m (half of the locations) or ±100 m. Based on ground checks, Potvin (1998) estimated that the maximum error was 25 and 100 m, respectively, and that this would result in about 26% of the locations being placed in an incorrect habitat type, taking into account the spatial error and the individual size of habitats on the map. Two types of home ranges, computed with CALHOME software (Kie et al. 1996), were used for habitat selection analysis. The 95% minimum convex polygon delineated the entire winter range, and the 60% adaptive kernel described that part of the home range used most intensely (Fig. 2).

We developed a spatial database with a raster structure and managed it using GRASS 4.1 (U.S. Army Construction Engineering Research Laboratories 1993) and GRASSLAND 1.1 (Logiciels et Applications Scientifiques 1996) software. Forest maps at a scale of 1:20,000 (MER

Figure 1. Aerial view of an area clearcut with the protection of regeneration cutting method, showing equally spaced harvesting trails to protect advanced regeneration and the shrub and herbaceous layers between trails.

1984) and clearcut delineations from 1:15,000 aerial photos were digitized in Arc/Info vector format (Environmental Systems Research Institute 1987) and rasterized with a 10 × 10 m pixel with Genamap and Genacell (GENASYS 1991). Home ranges were imported in ASCII vector format in the database and rasterized. We groundchecked the forest map and concluded that coniferous cover type and age class were relatively accurate variables and that crown closure or height were not (Potvin et al. 1999). Therefore, the forest layer was classified into eight terrestrial habitat types (Table 1).

Habitat selection was analyzed at the stand and landscape levels. At the stand level, we compared habitat available inside the home range (95% polygon) with sites used by the animal (telemetry locations) to identify habitat types that were preferred or avoided. Our first analysis at that scale was based on individual telemetry locations as the sample units and tested the hypothesis that telemetry locations were randomly distributed inside the home range. As suggested by Neu et al. (1974) and White and Garrott (1990), we used a chi-squared test between the number of locations observed (O_i) in each habitat type (i = 1–8) and the number expected (E_i) if the distribution is random: $E_i = O \times$ (area of type i/total area of the home range), where $O = \Sigma\, O_i$. A Bonferroni-type interval was computed to identify selected habitat types and to control for Type I error.

Our second analysis at the stand scale considered each animal the sample unit. As suggested by Alldredge and Ratti (1986, 1992), we used a Friedman nonparametric test that is equivalent to an analysis of variance with a complete randomized block design (i blocks × k treatments) based on ranks (Conover 1980). In this case, individual martens were the blocks and the habitat types were the treatments. Selected habitat types were identified by computing a Bonferroni interval (Siegel & Castellan 1988) and comparing the interval against a control, the control being an animal that would select habitats according to the null hypothesis of no affinity for a particular habitat. The Friedman test was applied to the Strauss selection index (Strauss 1979), as suggested by Alldredge and Ratti (1992), and the Chesson index

Figure 2. General forest landscape of the study area, radiotelemetry locations (+), and home ranges (95% polygon, larger; 60% kernel, smaller) of four martens. Regenerating stands (<20 years), mostly 1992–1994 clearcuts, are white.

(Chesson 1983; Manly et al. 1993). These indices were computed as follows:

$$\text{Strauss index} = Pu_i - Pa_i \text{ and}$$
$$\text{Chesson index} = (Pu_i/Pa_i)/(\Sigma_{i=1,k} Pu_i/Pa_i),$$

where Pu_i is the proportion of telemetry locations in habitat type i and Pa_i is the proportion of habitat type i in the home range.

At the landscape level, we wanted to determine whether the marten selects an unusual habitat mosaic from the entire study area. Delineation of the study area is critical at such a level (Johnson 1980; Aebischer et al. 1993). In our study, this area was defined as the area encompassing all home ranges and the location of all trapping sites to which a 500-m influence zone was added. At that scale, we pooled habitats BS3060, BS6080, BS80+ (black spruce), and CMC (other coniferous and mixed coniferous) into a single habitat type (coniferous-mixed-coniferous > 30 years) because we found no pronounced selection at the stand level. We also pooled coniferous-mixed-coniferous (C) and deciduous-mixed-deciduous (D) types into a general uncut forest >30 years habitat type (C+D) to compute some configuration metrics because martens preferred both types at the landscape level.

We used a sampling design based on random windows to test habitat selection at the landscape level. With this approach, the attributes of the home range are compared to those of the landscape computed from a large number of random blocks. To make valid comparisons, the size of the random mosaics should be of the same order as that of the home ranges. Based on the frequency distribution of marten home ranges, three sizes were used: 289 ha (home ranges <500 ha), 729 ha (home ranges = 500–950 ha), and 1156 ha (home ranges > 950 ha). We generated 100 random-square mosaics for each size class and compared landscape metrics between that sample and marten home ranges. Because logging modified the landscape during our study, we made separate analyses for the 1992–1993 and 1993–1994 winters. A variety of habitat composition and spatial configuration metrics was computed with FRAGSTATS (McGarigal & Marks 1995). Home ranges and random mosaics were exported as ASCII files and imported

Table 1. Description of the habitat types for martens in the study area in western Quebec.

Site code	Habitat type (age in years)	Forest composition	Vegetation survey (n plots)	Coarse woody debris (% interception)		Coniferous stems 0–1.3 m (stems/ha)		Lateral cover (%)	
				x̄	SD	x̄	SD	x̄	SD
BS3060	black spruce (30–60)	coniferous basal area >75% total and black spruce ≥50% coniferous	200	5.7 A*	6.5	1920 A	1960	73 A	22
BS6080	black spruce (60–80)	coniferous basal area >75% total and black spruce ≥50% coniferous	110	5.5 A	7.5	1430 BC	1450	no survey	
BS80+	black spruce (>80)	coniferous basal area >75% total and black spruce ≥50% coniferous	130	3.4 B	4.4	1590 AB	1180	71A	21
CMC	other coniferous and mixed coniferous (>30)	coniferous basal area ≥50% total	no survey						
D	deciduous and mixed deciduous (>30)	coniferous basal area <50% total	100	2.4 B	3.0	1635 AB	2320	83	11
CR	closed regenerating stands (<20)	mostly 1992–1994 clearcuts with dense regeneration; also budworm openings	73	7.5AC	7.7	950 CD	1440	56	28
OR	open regenerating stands (<20)	mostly 1992–1994 clearcuts with sparse regeneration; also older clearcuts	77	9.4 C	11.5	470 D	1380	31	16
NP	nonproductive lands	bogs and alder stands	no survey						

*Means with the same letter are not statistically different, one-way analysis of variance and Duncan test ($p > 0.05$).

into FRAGSTATS for analysis. Water was considered background (no value), and the mosaics evaluated had no border (strip of land surrounding the mosaic of interest).

Eight metrics were computed: %LAND, proportion of each habitat type in the total area; AWMSI, area-weighted mean shape index (C and C+D types); C%LAND, core area (C and C+D types) with a 50-m interior buffer; PD, patch density (C and C+D types); MNN, mean nearest-neighbor distance (C and C+D types); MPI, mean proximity index (C and C+D types) with a 200-m search radius; TECI, proportion of contrasted edge between OR/C, OR/C+D, CR/C, and CR/C+D types; and IJI, interspersion index (C and C+D types). These metrics were selected because they expressed the important aspects of marten habitat in terms of composition (%LAND), patch shape and/or size (AWMSI, C%LAND), patch fragmentation and isolation (PD, MNN, MPI, IJI), and edge effects (TECI). Because the distribution of many landscape metrics was far from normal, we used Mann-Whitney tests for statistical comparisons between marten home ranges and random mosaics of similar size.

Habitat Survey

To describe black spruce (BS3060, BS6080, BS80+), deciduous-mixed-deciduous (D), closed regenerating (CR), and open regenerating (OR) habitat types, we made a ground survey of three variables that express stand structure. This survey was concurrent with the validation of the forest map and used the same sampling plan (Potvin et al. 1999). We measured coarse woody debris 0–1.3 m from the ground by an intercept technique along a 20-m transect by counting all broken trees, logs, stumps, and limbs (including coniferous needles) with a diameter of >9 cm. Coniferous saplings and trees (black spruce and balsam fir) with continuous live limbs between 0 and 1.3 m from the ground were tallied in a 2 × 20 m plot. Lateral cover was evaluated with a 2-m profile board (Nudds 1977).

Results

Stand-Scale Habitat Selection

Our approach for measuring stand-level habitat selection, based on individual telemetry locations as sampling units, gave similar results for both winters (Fig. 3). D habitat was preferred ($p < 0.05$), whereas there was no selection for coniferous habitat types of any age class. OR stands were avoided ($p < 0.05$), but CR stands were used in proportion to their availability. For our second approach, with individual martens as the sampling units, selection by martens remained statistically significant for one habitat type only, OR, which was avoided by most

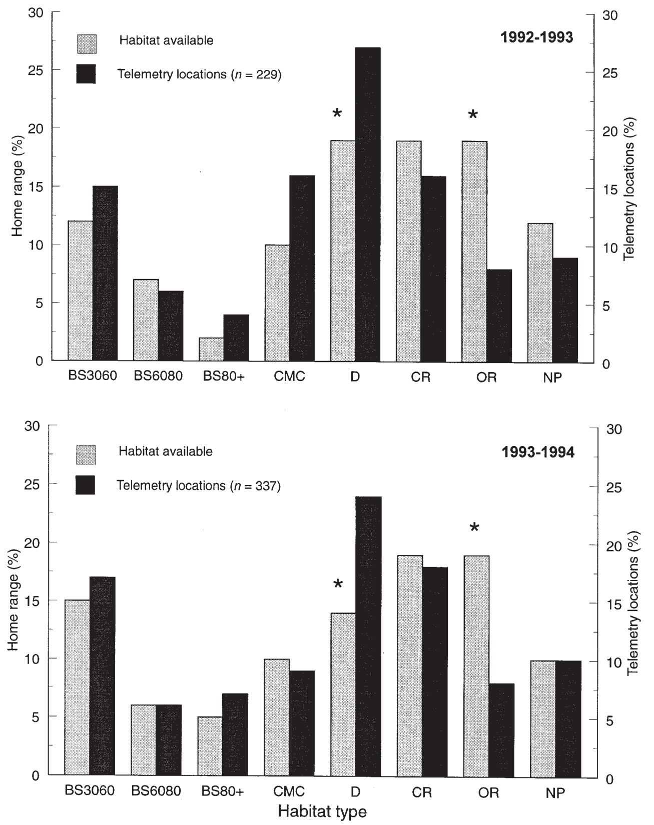

*Figure 3. Comparison between the proportion of each habitat type in marten home ranges (95% polygon), and the distribution of telemetry locations by habitat type during the winters of 1992–1993 and 1993–1994. Habitat types are defined in Table 1. The Neu test indicates a significant difference (*p *< 0.05) for deciduous-mixed-deciduous (D) and open regenerating (OR) habitat types for both winters.*

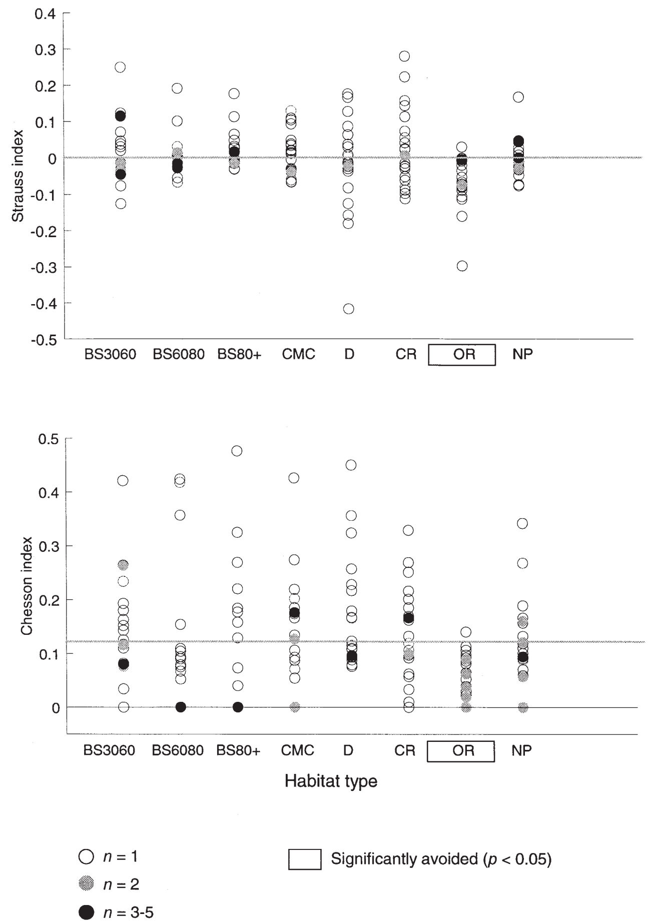

*Figure 4. Marten (*n *= 20) selection indices (Strauss and Chesson) for each habitat type in the study area. Each dot corresponds to one or more animals. Values above the horizontal line indicate habitat types preferred; those below the line indicate habitat types avoided. Habitat types are defined in Table 1.*

animals ($p < 0.05$; Fig. 4). Although D type was preferred by some martens, most animals showed no preference. Strauss and Chesson indices gave the same results, but the range of selection values seems larger with the Chesson index.

Landscape-Scale Habitat Selection

An example of our random window sampling design for testing habitat selection at the landscape level is shown in Fig. 5. Most 60% kernel home ranges belonged to the <500-ha area class and generally gave similar results over both winters (Table 2). Compared to random mosaics, 60% kernels contained a larger proportion of D habitat and fewer OR stands. C habitat was also preferred in 1993–1994. Differences were noted between kernel home ranges and random mosaics for some configuration metrics: kernels had a larger proportion of core area in C+D forest and less edge between OR and C or OR and C+D habitat types.

Home ranges described by the 95% polygon belonged to three size-area classes. Only the two smaller classes showed significant differences with random mosaics (Table 2). Results between both winters are less consistent for the 95% polygons than for the kernels. D habitat was preferred (<500 ha class, both years) and OR stands were avoided (1993–1994 only). Most noteworthy statistical differences for configuration metrics include a larger shape index for C+D patches in 95% polygons (both winters), a greater amount of core area in uncut forest (<500 ha class, both winters), longer nearest-neighbor distances between patches (C type, 500–950 class in 1992–1993, <500 ha class in 1993–1994); and less edge between OR and C+D habitat types (1993–1994).

The proportion of C+D habitat in the home range was inversely related to the size of the home range, both for the 60% kernel ($r = -0.78$) and the 95% polygon ($r =$

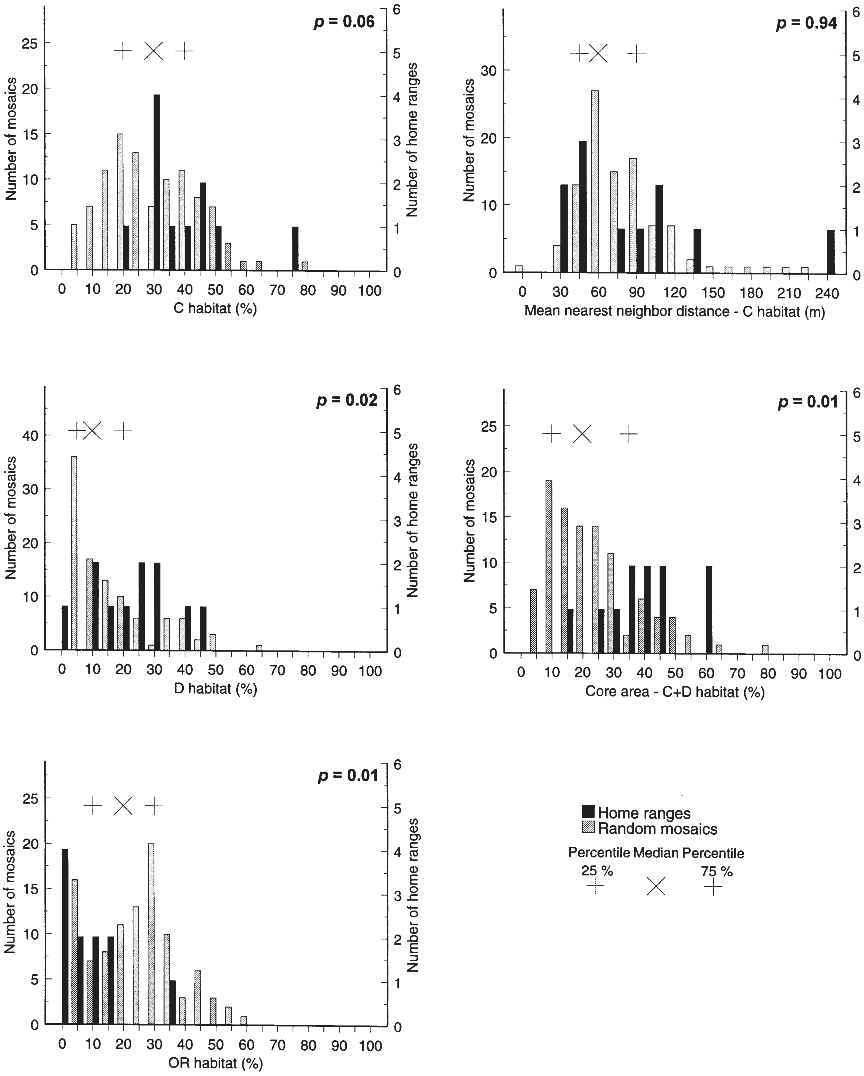

Figure 5. Frequency distribution of five landscape metrics for 100 random square mosaics of 289 ha in the study area in 1993–1994. The frequency distribution of the same metrics for 11 marten winter home ranges (60% kernels) in the same year, belonging to the class area of <500 ha, is also shown with the associated p *value of the Mann-Whitney test between both samples. The C habitat is coniferous-mixed-coniferous. See Table 1 for definitions of others.*

−0.47) (Fig. 6). Conversely, smaller home ranges contained a lower proportion of OR stands and OR and CR stands combined (OR+CR) (60% kernels, $r = 0.74$–0.76; 95% polygon, $r = 0.44$).

Habitat Survey

The amount of coarse woody debris was low in older black spruce (BS80+) and D habitat types (2–3% ground interception), intermediate in young or mid-age black spruce stands (BS3060, BS6080; 6%), and higher in recently cut stands (8–9%) (Table 1). The number of coniferous stems with continuous limbs 0–1.3 m from the ground was similar in D and black spruce stands (1440–1920 stems/ha), but D habitat had a denser lateral cover (83 vs. 71–72%). Compared with OR stands, CR stands had twice as many coniferous stems (945 vs. 470 stems/ha) and a more dense lateral cover (56 vs. 31%).

Discussion

In our clearcut boreal landscape, martens were selective for their winter habitat both at the stand and the landscape level. At the stand level, we hypothesized that in their home ranges martens would (1) avoid clearcut areas and (2) prefer mature or overmature coniferous stands. This was partially true only for our first hypothesis, with martens clearly selecting against OR stands composed mostly of recent clearcuts with a sparse regeneration. Many studies report that martens avoid recent cutovers (Soutiere 1979; Brainerd et al. 1994; Thompson & Harestad 1994; Alvarez 1996). The CR stands, however, were used in proportion to their availability. The CR habitat type resulted from recent clearcuts in coniferous or mixed coniferous stands partially affected by the budworm epidemic that prevailed from 1974 to 1976. As opposed to OR, vegetation surveys indicated that CR had a more abundant coniferous regeneration

Table 2. Statistical comparison between random mosaics (n = 100 by area class and by winter) and marten home ranges in winters 1992–1993 and 1993–1994 according to the type of home range.[a]

	1992-1993				*1993-1994*			
	60% kernel[c]		*95% polygon[d,e]*		*60% kernel[c]*		*95% polygon[d,f]*	
Metric and habitat type[b]	*<500 ha (n = 7)*	*500–950 ha (n = 1)*	*<500 ha (n = 4)*	*500–950 ha (n = 3)*	*<500 ha (n = 11)*	*500–950 ha (n = 1)*	*<500 ha (n = 5)*	*500–950 ha (n = 3)*
Percent habitat type (% LAND)								
C	0	0	0	0	+	0	0	0
D	++	0	+	0	++	0	++	0
CR	0	0	0	0	0	0	0	0
OR	−	0	0	0	−−	0	−	−
NP	0	0	0	0	0	0	0	0
Shape index (AWMSI)								
C	0	0	0	−−	0	0	0	0
C+D	0	0	+	++	0	0	++	+
Core area (C%LAND)								
C	0	0	0	0	0	0	0	0
C+D	++	0	+	0	++	0	++	0
Patch density (PD)								
C	0	0	0	0	0	0	−	0
C+D	0	0	0	0	−	0	−−	0
N-neighbor (MNN)								
C	++	0	0	++	0	0	++	0
C+D	0	0	0	0	0	0	0	0
Proximity (MPI)								
C	0	0	0	0	0	0	−	0
C+D	0	0	0	0	0	0	0	0
Edge (TECI)								
CR/C	0	0	0	0	0	0	0	0
CR/C+D	0	0	0	+	0	0	+	0
OR/C	−	0	0	0	−−	0	−	0
OR/C+D	−	0	0	0	−−	0	−−	−
Interspersion (IJI)								
C	0	0	0	0	0	0	0	0
C+D	0	0	0	0	0	0	0	0

[a]*Mann-Whitney test between home ranges and random mosaics: ++, much higher value in home ranges* ($p < 0.05$)*; +, higher value in home ranges* ($p < 0.10$)*; 0, no difference* ($p > 0.10$)*; −, lower value in home ranges* ($p < 0.10$)*; −−, much lower value in home ranges* ($p < 0.05$)*.*
[b]*Habitat abbreviations: C, coniferous-mixed-coniferous; see Table 1 for definition of others.*
[c]*The 60% adaptive kernel (60% kernel) describes that part of the winter range used most intensely.*
[d]*The 95% minimum convex polygon (95% polygon) delineates the entire winter range.*
[e]*Results for one home range (male of unknown sex) belonging to the >950-ha area class are not presented because all comparisons are not significant* ($p > 0.10$)*.*
[f]*Results for four home ranges (one juvenile female, one female of unknown age, two adult males) belonging to the >950-ha area class are not presented because all comparisons are not significant* ($p > 0.10$)*.*

0–1.3 m high and a dense lateral cover. In balsam fir forests, Alvarez (1996) also noted that martens used recent cutovers at the sapling stage.

In their home range, martens did not select coniferous stands, even those that were mature or overmature, but preferred deciduous and mixed deciduous (D). About 60% of stands belonging to the D type issued from mixed coniferous stands where the recent budworm epidemic killed the balsam fir component. As a result, compared to coniferous stands they had a similarly dense coniferous undercover and lateral cover. In Maine and in Newfoundland, stands opened by a budworm epidemic also were used heavily by martens (Sturtevant et al. 1996; Chapin et al. 1997). Mixed coniferous stands were also preferred (track count) in the control block of Soutiere's (1979) study in Maine.

At the landscape level, we hypothesized that martens would select mosaics with (1) <20–30% area in clearcuts, (2) larger amounts of coniferous stands than random mosaics, and (3) less fragmentation. Our first hypothesis was readily met: OR stands were avoided and usually made up <20% of home ranges, and open or closed regenerating stands combined (OR+CR) made up <30–35%. In Maine the maximum proportion of cutovers in the home range was 40% for resident males and 31% for females (Chapin et al. 1998). In Utah Hargis and Bissonette (1997) noted that martens were absent from 9-km^2 blocks when the proportion of open areas (cutovers, natural openings) was above 25%. Thompson and Harestad (1994) hypothesized that dispersed cuttings in the landscape up to 20–30% would favor martens but that the population would decline rapidly above that level.

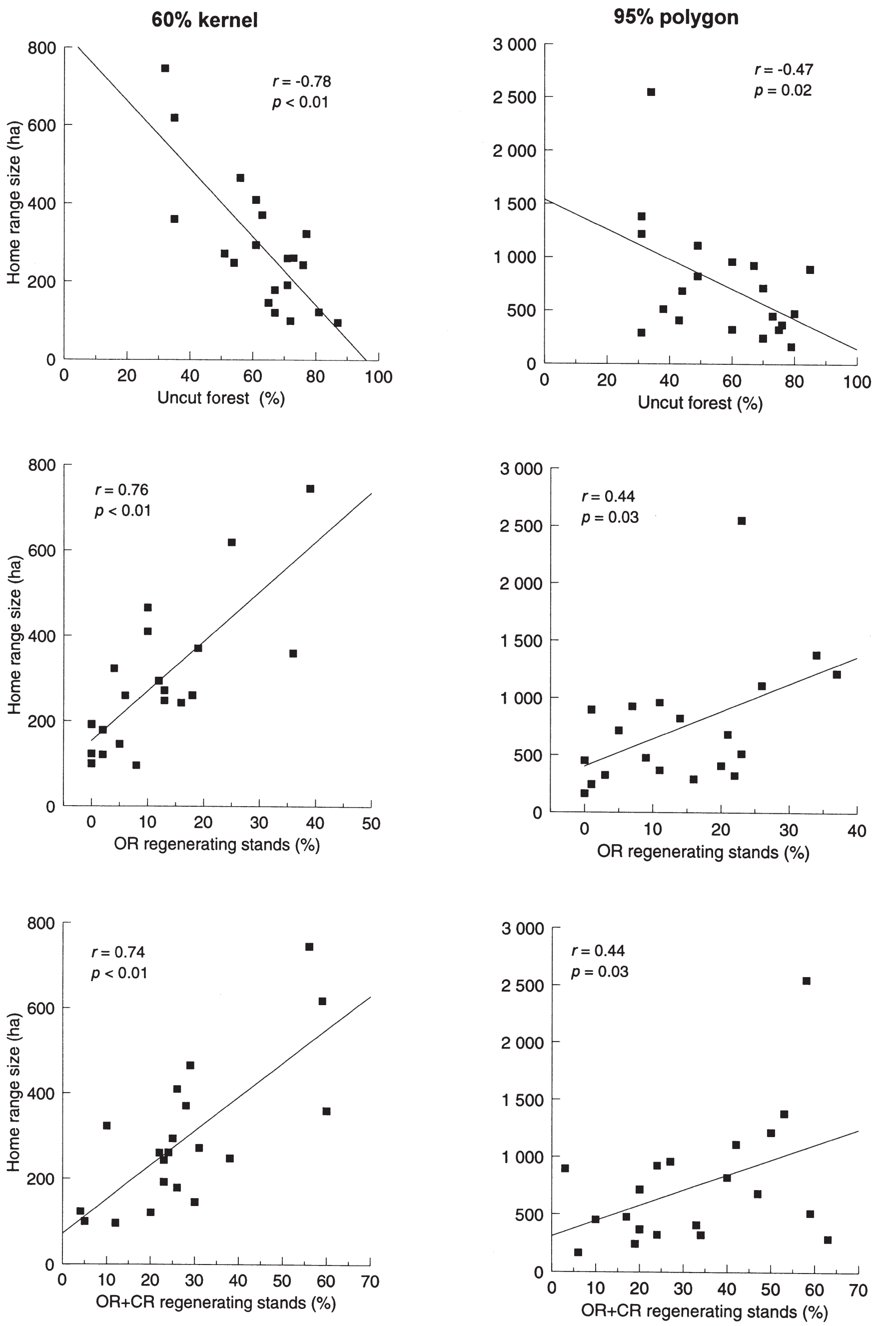

Figure 6. Proportion of uncut forest (C+D habitat type), open regenerating stands (OR), and open or closed regenerating stands combined (OR+CR), as related to the size of the home range. Habitat types are defined in Table 1. The 60% adaptative kernel (60% kernel) describes that part of the winter range most intensely used, and the 95% minimum convex polygon (95% polygon) delineates the entire winter range.

Based on three studies located far apart (Utah, Maine, Québec), we suggest that the maximum amount of clearcuts that the American marten can tolerate in its home range is about 30%.

The proportion of coniferous stands was larger in home ranges than in random mosaics in the winter of 1993–1994 (60% kernels) but was not different in the winter of 1992–1993. Contrary to our initial hypothesis, D habitat was preferred at the landscape level, as was the case at the stand level. This result, consistent for the 60% kernel and the 95% polygon for both winters, can be explained by the dense coniferous shrub layer in these stands established after the budworm epidemic. Few studies of landscape habitat selection for martens have been conducted. In British Columbia Lofroth (1993) reports martens select for mature or overmature forests. In Maine there was no selection at the landscape level in Baxter Park, a conservation area, but forest cover >6 m in height was strongly selected in a neighboring study area with large clearcuts (Chapin et al. 1997, 1998).

Fragmentation was lower in home ranges than in random mosaics according to the most significant configuration metrics. Core area in uncut forest (C+D), which is related to the size and shape of forest patches, was much higher in home ranges. The contrasted edge metric between OR stands and C+D habitat measured the proportion of the perimeter of uncut forest patches directly in contact with OR habitat. This metric was significantly lower in the home ranges. Such a result was predictable, however, because home ranges already contained more C+D and less OR habitat, and both fragmentation metrics are strongly related to habitat composition (r = 0.97 between the core area of C+D type and the proportion of this habitat type; r = 0.81 between the contrasted edge between OR and C+D types and the proportion of the OR habitat type).

Management Implications

Contrary to the findings of most studies of marten habitat, martens in our study area did not select coniferous stands, even those that were mature or overmature, in their home range, but they preferred deciduous and mixed deciduous forests at the stand and landscape levels. Martens are described as being selective for mature or overmature coniferous stands because these areas provide predator avoidance, prey abundance, and needed structural elements (Bissonette et al. 1989; Thompson 1991; Thompson & Harestad 1994). In eastern North America, the most important predators for martens are the coyote (*Canis latrans*), red fox (*Vulpes vulpes*), fisher (*Martes pennanti*), and some birds of prey (Strickland & Douglas 1987; Buskirk & Ruggiero 1994). Climbing trees is their strategy to escape terrestrial predators (Strickland & Douglas 1987; Storch et al. 1990), and ground cover makes visual detection by birds of prey more difficult. To minimize predation, martens need a habitat with well-distributed tree stems and a dense coniferous shrub cover, not necessarily a mature or overmature stand.

Red-backed voles (*Clethryonomys gapperi*) are the usual prey for martens. This species is present throughout all successional stages in black spruce and balsam fir stands, even immediately after clearcutting with protection of regeneration (Génier & Bergeron 1996; Gagné 1997). The snowshoe hare is often the marten's major prey in eastern North America in winter (Thompson & Colgan 1990, 1994); snow tracking in our study area indicated that marten hunting activity strongly favored that prey species (Potvin 1998). Showshoe hares may be abundant in overmature forest (Thompson 1988) but are generally found in larger numbers in young forests (Litvaitis et al. 1985; Koehler 1990). Therefore, based on prey abundance, mature or overmature forests cannot be considered a strict requirement for martens.

The most important structural elements for marten habitat in winter are coarse woody debris and coniferous saplings (Allen 1982; Hargis & McCullough 1984; Corn & Raphael 1992; Alvarez 1996). These elements enable access to small mammals living under snow and are needed to establish resting sites. Except in recent clearcuts, the amount of woody debris was low (<6%) in black spruce and D type forests. In black spruce stands, it was even lower in older stands (>80 years) than in younger ones. As a result of the past budworm epidemic, coniferous saplings were as numerous in mixed and deciduous stands as in coniferous stands. Contrary to western North American forests, whose longevity exceeds 300–400 years, black spruce stands do not have structural advantages for martens when they approach maturity. These structural characteristics are more prevalent in stands affected by the spruce budworm in terms of horizontal structures (small natural openings) and vertical structures (herbaceous and shrub layers, snags, coarse woody debris).

Chapin et al. (1997) suggest that martens do not prefer or require dense coniferous cover and that vertical and horizontal structures are more important than age or species composition. Based on our results and those of Chapin et al. (1997, 1998), such a description might apply throughout eastern North America, except possibly Newfoundland. On that island, red-backed voles are not present, and the only abundant small mammal, the meadow vole (*Microtus pensylvanicus*), is absent or rare in younger or second-growth forests (Thompson & Curran 1995; Sturtevant & Bissonette 1997).

The preference for mixed and deciduous stands and the prevalence of martens in recent clearcuts with dense regeneration seems to be related to structural characteristics and to prey abundance. Both habitat types were affected by the budworm epidemic. Even after clearcutting with protection of regeneration, closed regenerating stands are more related to a partial cut than a clearcut. Martens can be maintained after partial cut (Soutiere 1979; Steventon & Major 1982) or in areas where groups of trees and coarse woody debris are left after cut, as suggested by Hargis and McCullough (1984), to preserve marten habitat. Red-backed voles are prolific in spruce budworm stands (Gagné 1997), which are also favorable for snowshoe hares in terms of cover and browse.

Are martens and clearcutting compatible? Our results confirm that large clearcuts in boreal forest, even with the protection of regeneration cutting method, have a negative effect on martens. This species appears fairly intolerant of habitat fragmentation and cannot tolerate more than 30–35% cutovers (OR + CR) in its home range. As suggested by Bissonette et al. (1989) and Thompson and Harestad (1994), a landscape management approach is needed to protect or improve marten habitat. Where the objective is to maintain martens at a local scale in black spruce forests, we suggest that ≥50% uncut forest (>30 years old) be preserved inside 10-km^2 units and that <30% of the area be clearcut over a 30-year period. Uncut forest patches should be large (>100 ha) to maximize core area and minimize edge with open cutovers. Clearcuts need not be small because large cutovers create less fragmentation (Li et al. 1993) and are needed to recreate large forest blocks within 30 years. Where lakes and watercourses are abundant such as on the Canadian shield, preserving riparian buffer zones should offer good connectivity between forest patches. We did not examine source-sink dynamics (Pulliam 1988), which can be important on a regional scale. For example, are large uncut blocks and trapping preserves needed to maintain viable populations? Future research is needed to answer such fundamental questions.

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